

# FLOWER AND FRUIT BIOLOGY IN SOUTHERN SPANISH MEDITERRANEAN SHRUBLANDS<sup>1</sup>

JAVIER HERRERA<sup>2</sup>

## ABSTRACT

Flower and fruit biology was studied in a coastal, southern Spanish scrub community composed of 30 plant taxa. Data on breeding systems; rewards offered to vectors; flower, fruit, and seed sizes; and fruiting intensities are reported. Most taxa in the community have insect-pollinated, hermaphroditic flowers that are largely unspecialized in morphology. Dioecious species are relatively well represented (27% of the total), as are vertebrate-dispersed species (43%). Bagging experiments demonstrated that pollinators were required for maximum fruit production, but the existence of incompatibility systems was not tested. When the relationship between fruiting intensity and the ability to perform vegetative regeneration was investigated, it was found that sprouting taxa had, on average, lower fruit production than those that were unable to sprout. Low fruit production is discussed in relation to reproductive allocation trade-offs.

Mediterranean-type vegetation has been the subject of research for investigators who wish to emphasize convergence phenomena in geographically distant areas with similar environmental factors (Specht, 1969; Mooney & Dunn, 1970; Cody & Mooney, 1978). Also, a great emphasis has been put upon plant development and the adaptive features of plants in this highly seasonal climate (Mooney & Parsons, 1973; Mooney et al., 1974; Kummerov, 1983). Comparatively little is known, however, about other characteristics in the biology of mediterranean species, such as their reproductive biology. The paucity of information is particularly noticeable with respect to plants living in the Mediterranean region itself (but see C. M. Herrera, 1981, 1984; Jordano, 1982, 1984, for plant-frugivorous bird relationships, and J. Herrera, 1985, for nectar secretion patterns in scrub). Some information is available for mediterranean areas in America, Australia, and South Africa (for example, Moldenke, 1975; Specht et al., 1981; Kruger, 1981). But in spite of this, our present knowledge of the reproductive biology of mediterranean shrublands is low compared to our knowledge of tropical (for example, Frankie et al., 1974, 1983; Heithaus, 1974; Bawa, 1979; Bawa & Opler, 1975; Opler et al., 1980) and temperate plant communities (for example, Mosquin, 1971; Kevan, 1972; Pojar, 1974; Reader, 1977; Primack, 1983).

This paper presents part of a study designed

to investigate the reproductive biology of a southern Spanish sclerophyllous scrub community. Flower and fruit features in a number of taxa are used to elucidate reproductive patterns. The relationship between sprouting behavior (the production of new stems from established rhizomes, lignotubers, or burls; James, 1984) and pollination-reproduction variables is also investigated. Pollination relationships at the community level will be dealt with elsewhere (J. Herrera, in prep.).

## STUDY AREA AND METHODS

This study was conducted in the Doñana Biological Reserve (Doñana National Park, Spain). The reserve is located on the Atlantic coast of southwestern Spain, in an area with a mediterranean-type climate where the vegetation is composed mainly of mediterranean sclerophyllous shrublands with some planted pine woods. Annual precipitation averages 537 mm. Mean annual temperature is 16°C, January being the coolest month (9.8°C) and July the hottest (24.6°C). Temperatures rarely descend below zero, and summer drought covers five months on average (May through September). The soil is sandy, and maximum elevation above sea level is 30 m.

Basically the vegetation encompasses two types of scrub formations, distributed according to topographic and edaphic factors. Where the level of the underground water table is relatively near

<sup>1</sup> This study received financial support from the Spanish Comisión Asesora de Investigación Científica y Técnica (CAICYT), through a grant (82/264) to Salvador Talavera (Departamento de Botánica, Facultad de Biología, Universidad de Sevilla). I thank Dr. P. E. Gibbs for correcting the English, and two reviewers for helpful comments on the manuscript.

<sup>2</sup> Departamento de Botánica, Facultad de Biología, 41080 Sevilla, Spain.

soil surface, the scrub becomes dominated by hygrophytic species (heath). Otherwise, a highly xerophytic scrub vegetation is found (see Allier et al., 1974; Rivas-Martínez et al., 1980). The most representative species, both in hygrophytic and xerophytic scrub, were selected for study giving a total of 30 taxa. From December 1982 through March 1984 the study plot was visited weekly, and data on flowering phenology, pollination relationships, and flower-fruit biology of the species were gathered. Here I report only on aspects of flower and fruit biology.

Individual plants or branches were marked before flowering, and their area estimated from maximum and minimum diameters. Flowers were counted every week during the time of study, and the maximum numbers registered for the plants of a species were averaged to give an estimate of flower production per unit area.

Fresh samples of flowers and fruits of all taxa were taken to determine the most outstanding external features, such as dimensions, color, and sex. Ten to 20 flowers of each species were measured (length, maximum and minimum diameters), and 20 to 500 complete flowers without their pedicels were air dried and weighed. The maximum dimension of a flower was found to be directly correlated with its dry weight ( $r_s = 0.806$ ,  $N = 30$ ,  $P < 0.001$ ). Therefore dry weight has been used subsequently as an estimate of flower size, since it is less dependent on the architecture of the corolla than on the maximum dimension. Pollination modes of taxa were determined from external features and visitor censuses (J. Herrera, in prep.). Flower forms were referred to those of Faegri and van der Pijl (1979).

Pollen production and the number of ovules in the ovary of each flower were determined for 10 to 15 flowers per plant species. Ovules were counted under a dissecting microscope. Pollen production was assessed in the same flowers by macerating one or two anthers in a known volume of detergent-safranin solution and counting the number of grains in 10 replicates of 5  $\mu$ l. Pollen-ovule ratios of hermaphroditic species were then compared with those given by Cruden (1977).

To investigate nectar secretion, flowers were observed in the field and in the laboratory under a dissecting microscope. In doubtful cases, the arrival of insect visitors to flowers was precluded by bagging branches with white nylon mesh; flowers were examined after 24 hours and, when possible, the accumulated nectar was quantified.

The volume per flower was measured by the length of the column, in mm, inside 5  $\mu$ l micropipettes. Concentration, on a weight: weight basis, was measured in two ATAGO refractometers (models N1 and N2) compensated to ambient temperature. The milligrams of nectar sugar plus diluted solids (Inouye et al., 1980) were computed by the product of volume  $\times$  concentration (Bolten et al., 1979).

Percent fruit production in open pollinated flowers of the species was estimated from flower and ripe fruit counts on marked branches. In the same individual plants that were used to estimate percent fruiting, some branches were also bagged with white nylon mesh (or with glassine paper bags in anemophilous taxa) to determine fruiting intensities when pollinators were excluded. Bagging experiments were not carried out with dioecious taxa. Samples of fruit were collected and oven dried to a constant weight, and the number of seeds, along with the weights of the whole fruit, all seeds, and that of an individual seed were averaged and recorded. Notes on fruit and flower predation were also taken and, when possible, the agents responsible were identified.

The ability to perform vegetative regeneration after complete destruction of aboveground biomass (sprouting) was assessed for every species. Data on sprouting of these species were derived from careful observations carried out in the study area on plants damaged by fire, herbivores, or human disturbance during the years 1982 through 1985.

## RESULTS

### FLOWER BIOLOGY

The names of the species studied, together with their most distinctive floral features, are summarized in Table 1. Our set of mediterranean plants consists of 30 taxa in 17 families and 25 genera. Most families contribute one or two species, with only Cistaceae, Leguminosae, Labiatae, and Ericaceae being relatively well represented (5, 4, 3, and 3 species, respectively).

Pollination by insect vectors is dominant in the community, where entomophilous species account for more than 80% of the total (Table 1). Only five species rely on wind for pollen dispersal. Hermaphroditism is the most common breeding system with 21 taxa (70%), although dioecious species are relatively well represented (27%). *Thymus tomentosus* is the only species with a different sexual condition (gynodioecy).

TABLE 1. Floral attributes of 30 scrub species. (BS, breeding system; PM, pollination mode; FF, flower form; DW, dry weight of individual flowers, in mg; P, mean number of pollen grains per flower, in thousands; P:O, pollen-ovule ratio.) Flower number indicates the mean number in individual plants at peak bloom per m<sup>2</sup>, followed by the standard error; number of plants is indicated in parentheses. When there are differences among sexes in dioecious taxa, the value corresponding to female flowers is given first.

Species	BS <sup>1</sup>	PM <sup>2</sup>	FF <sup>3</sup>	Color <sup>4</sup>	Re-ward <sup>5</sup>	DW	P	P:O	Flower Number	Pre-dation
<i>Armeria velutina</i> Welw. ex Boiss. & Reuter	H	E	d	p	N	2.0	1	979	2,553 ± 621 (10)	-
<i>Asparagus aphyllus</i> L.	D	E	d	g	N	0.8-1.5	37	-	599 ± 237 (10)	+
<i>Calluna vulgaris</i> (L.) Hull	H	E	b	p	N	2.3	24	1,047	16,495 ± 4,847 (12)	-
<i>Chamaerops humilis</i> L.	D	A	a	y	-	8.3-4.1	214	-	366 ± 118 (10)	-
<i>Cistus libanotis</i> L.	H	E	d	w	P	24.5	55	2,482	177 ± 27 (10)	-
<i>Cistus salvifolius</i> L.	H	E	d	w	P	65.5	106	1,908	68 ± 12 (10)	-
<i>Corema album</i> (L.) D. Don	D	A	a	brown	-	0.5-0.1	229	-	-	-
<i>Cytisus grandiflorus</i> D.C.	H	E	f	y	P	22.4	69	6,179	244 ± 53 (10)	-
<i>Daphne gnidium</i> L.	H	E	t	cream	N	2.8	9	9,040	854 ± 301 (10)	+
<i>Erica ciliaris</i> L.	H	E	b	p	N	4.6	35	129	52 ± 23 (7)	+
<i>Erica scoparia</i> L.	H	A	b	g	-	0.8	92	2,008	56,902 ± 13,699 (5)	+
<i>Halimium commutatum</i> Pau	H	E	d	y	P	11.6	13	2,024	256 ± 41 (10)	-
<i>Halimium halimifolium</i> L. (Willk.)	H	E	d	y	P	26.8	55	1,179	89 ± 21 (9)	-
<i>Helianthemum croceum</i> (Desf.) Pers.	H	E	d	y	P	15.4	53	3,039	498 ± 114 (10)	-
<i>Helichrysum picardii</i> Boiss. & Reuter	H	E	d	y	P	0.1	2	2,075	26,561 ± 8,488 (10)	-
<i>Lavandula stoechas</i> L.	H	E	t	purple	N	1.5	4	1,030	4,683 ± 669 (10)	-
<i>Lonicera periclymenum</i> L.	H	E	t	cream	N	19.1	10	850	48 ± 3 (4)	-
<i>Myrtus communis</i> L.	H	E	brush	w	P	16.8	599	12,323	266 ± 72 (4)	-
<i>Osyris alba</i> L.	D	E	d	g	N	2.6-1.8	5	-	3,497 ± 754 (8)	-
<i>Osyris quadripartita</i> Salzm. ex Decne	D	E	d	g	N	1.8-0.8	3	-	7,281 ± 1,897 (10)	-
<i>Phillyrea angustifolia</i> L.	H	A	d	w	-	1.6	72	71,932	11,727 ± 2,861 (7)	-
<i>Pistacia lentiscus</i> L.	D	A	a	p-y	-	0.4-2.1	35	-	-	-
<i>Rhamnus lycioides</i> L.	D	E	d	g	N	0.6	15	-	-	-
<i>Rosmarinus officinalis</i> L.	H	E	t	w	N	2.7	5	1,346	2,226 ± 403 (14)	-
<i>Rubus ulmifolius</i> Schott.	H	E	d	p	N	53.7	54	11,022	13 ± 2 (10)	-
<i>Smilax aspera</i> L.	D	E	d	w	?-P	1.8-1.4	13	-	527 ± 616 (11)	-
<i>Stauracanthus genistoides</i> (Brot.) Samp.	H	E	f	y	P	5.1	20	3,579	970 ± 245 (10)	-
<i>Thymus tomentosus</i> Willd.	G	E	t	w	N	0.6-0.7	5	1,148	2,859 ± 531 (8)	-
<i>Ulex minor</i> Roth.	H	E	f	y	P	3.0	13	1,824	687 ± 170 (14)	-
<i>Ulex parviflorus</i> Pourret	H	E	f	y	P	8.0	19	2,943	111 ± 44 (8)	-

<sup>1</sup> H, hermaphrodite; D, dioecious; G, gynodioecious.

<sup>2</sup> E, entomophilous; A, anemophilous.

<sup>3</sup> d, disc; b, bell; a, apetalous; f, flag-blossom; t, tube.

<sup>4</sup> p, pink; g, green; y, yellow; w, white.

<sup>5</sup> N, nectar; P, pollen

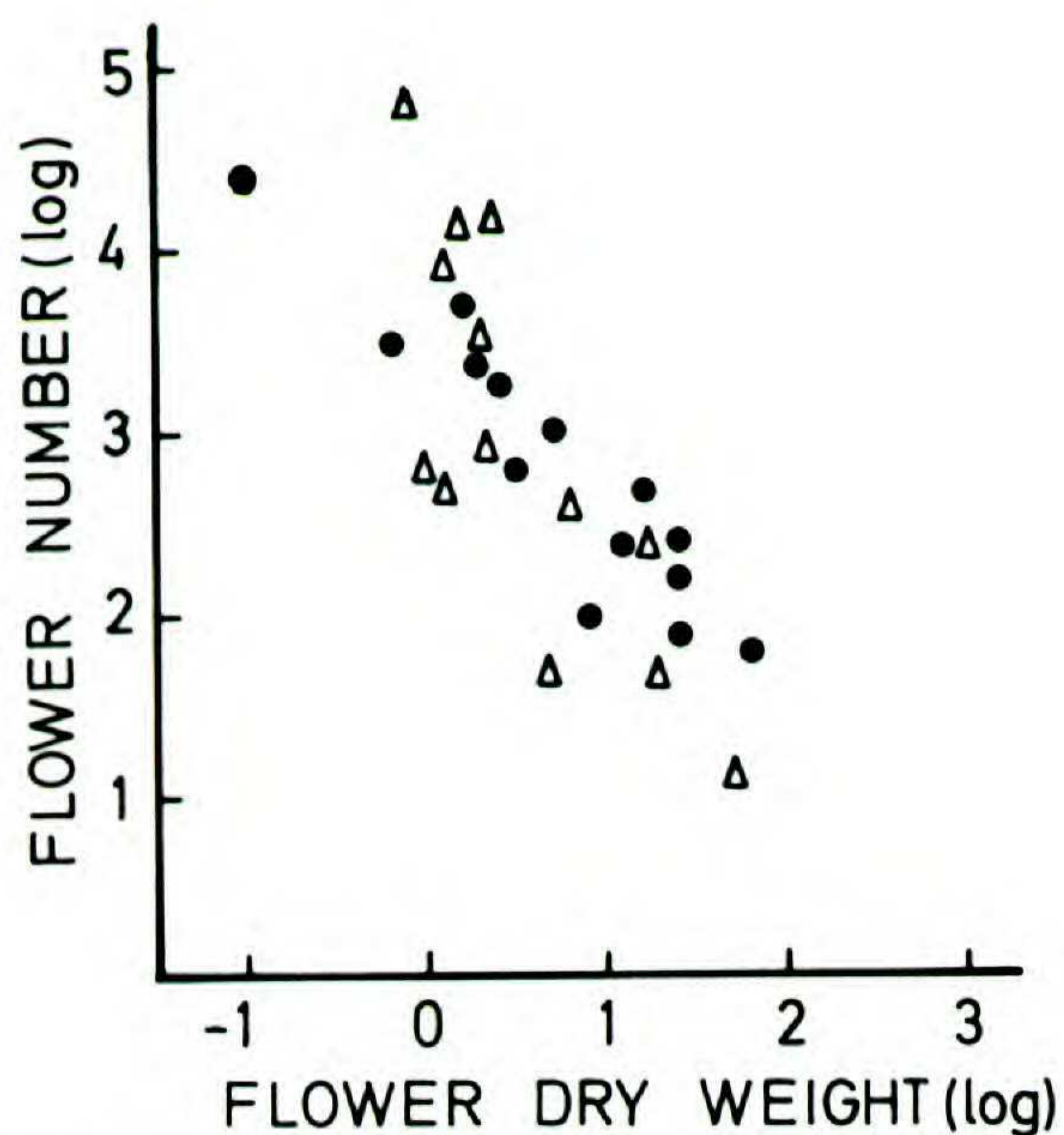


FIGURE 1. Relationship between the weight of an individual flower and the mean number of flowers per square meter in peak blooming plants. Triangles = sprouting taxa; circles = nonsprouting taxa.

Flower sizes (as dry weight of the complete flower) in the sample range between 2.2 mg for the female flowers of *Pistacia lentiscus* and 65.5 mg for *Cistus salvifolius*. More than 50% of the taxa have flowers of 5 mg or less in dry weight. Floral dry weight is not independent of the breeding system in this set of species. If taxa are segregated in two categories, less or more than 5 mg (a value that is near the median in the frequency distribution), dioecious taxa predominate in the lower class (8 out of 9), whereas hermaphroditic taxa are evenly distributed among the two classes (10 and 11, respectively). The differences are statistically significant ( $G = 5.04$ ,  $df = 1$ ,  $P < 0.025$ ).

The predominant flower morphology is of the dishbowl type (Faegri & van der Pijl, 1979), which is present in the Cistaceae and also in all the entomophilous dioecious taxa. Species in the Labiatae have short, tubular corollas; while the legumes present typical flag blossoms. The only long-tubed flowers are those of *Lonicera periclymenum*. Generally speaking, flowers are small and/or have corollas that impose little or no restriction on floral visitors (except for *L. periclymenum* and the legumes). All species in the Leguminosae and three in the Cistaceae have yellow flowers, which is the most common color (nine of total); whereas six species have white corollas. Many of these yellow- or white-flowered taxa offer pollen as the main reward to pollinators (Table 1). There are five species with pink flowers, which provide predominantly nectar as the reward.

Among entomophilous taxa, pollen and nectar are offered by approximately the same number of species (12 and 13, respectively). However, since wind-pollinated taxa are also occasionally used as a pollen source by insects (pers. obs.), this food material is more readily available in our community than is nectar, at least in terms of plant taxa. Furthermore, we have succeeded in quantifying the secretion in only six out of 13 species in which nectar is the main reward. These species were *Daphne gnidium* (0.17 mg sugar/flower per 24 hr.), *Erica ciliaris* (0.08 mg), *Lavandula stoechas* (0.15 mg), *Lonicera periclymenum* (2.00 mg), *Rosmarinus officinalis* (0.20 mg), and *Rubus ulmifolius* (1.20 mg). In the remaining seven species the yield of nectar sugar per flower per 24 hr. was too scarce to be quantified with our method (presumably less than 0.08 mg). Maximum concentration values ranged between 9.5% (*Erica ciliaris*) and 60% (*Rubus ulmifolius*); volumes per flower on a daily basis ranged between 0.9  $\mu$ l (*Lavandula stoechas*, *Daphne gnidium*) and 10  $\mu$ l (*Lonicera periclymenum*).

Pollen yield of the individual flowers is given in Table 1. The lowest is that of *Armeria velutina* ( $10^3$  grains) and the highest that of *Myrtus communis* ( $599 \times 10^3$ ), which has insect-pollinated, nectarless flowers of the brush type common in the Myrtaceae. Since pollen production is not independent of flower size, a more correct estimate of staminate effort on a per flower basis would be the number of pollen grains produced per milligram of flower dry weight (Relative Staminate Effort, RSE). Defined in this way, RSE is minimum for entomophilous taxa such as *Armeria velutina* (500) and *Lonicera periclymenum* (524). The former has dimorphic pollen grains and stigmas, and the latter has the most specialized (long-tubed, highly nectariferous) flowers in the sample. Maximum values of RSE are found in anemophilous species such as *Corema album* ( $2.3 \times 10^6$ ) and *Erica scoparia* ( $120 \times 10^3$ ). Mean RSE is significantly higher for anemophilous taxa than for entomophilous ones ( $U = 121$ ,  $N = 5$ ,  $25$ ,  $P < 0.001$ ).

Values of pollen-ovule ratios for hermaphroditic species are given in Table 1. In most taxa this ratio is greater than 2,000 and thus referable to the allogamous class of Cruden (1977). Only three species have pollen-ovule ratios lower than 1,000. Mean number of flowers for plants in peak bloom are also shown in Table 1. A highly significant relationship exists between flower num-

TABLE 2. Fruit and seed characteristics for 29 scrub species. Numbers in parentheses are sample sizes.

Species	Type <sup>1</sup>	Mean Number of Seeds	Mean Dry Weight (mg)			Pre- dation
			Whole Fruit	All Seeds	Individual Seed	
<i>Armeria velutina</i>	D	1	3 (50)	1	1 (50)	+
<i>Asparagus aphyllus</i>	F	1.2	46 (100)	23	19 (122)	+
<i>Calluna vulgaris</i>	D	3.6	2 (100)	0.2	0.1 (325)	-
<i>Chamaerops humilis</i>	F	1	1,364 (18)	781	781 (18)	+
<i>Cistus libanotis</i>	D	22.3	59 (20)	23	1 (445)	+
<i>Cistus salvifolius</i>	D	51	137 (12)	53	1 (612)	+
<i>Corema album</i>	F	3	57 (30)	35	12 (90)	-
<i>Cytisus grandiflorus</i>	D	6.9	214 (20)	39	6 (137)	-
<i>Daphne gnidium</i>	F	1	18 (75)	8	8 (75)	-
<i>Erica ciliaris</i>	D	17.9	5 (80)	0.2	0.01 (1,150)	+
<i>Erica scoparia</i>	D	6.5	1 (60)	0.1	0.02 (1,000)	+
<i>Halimium commutatum</i>	D	2.6	33 (20)	14	6 (52)	+
<i>Halimium halimifolium</i>	D	25.7	59 (20)	15	0.6 (514)	-
<i>Helianthemum croceum</i>	D	10.3	34 (15)	15	1 (155)	+
<i>Helichrysum picardii</i>	D	1	0.6 (750)	0.6	0.6 (750)	-
<i>Lavandula stoechas</i>	D	2.3	4 (50)	1	0.6 (114)	+
<i>Lonicera periclymenum</i>	F	2.3	52 (30)	15	7 (30)	-
<i>Myrtus communis</i>	F	5.7	108 (75)	56	10 (430)	-
<i>Osyris alba</i>	F	1	157 (30)	90	90 (30)	+
<i>Osyris quadripartita</i>	F	1	131 (75)	73	73 (75)	+
<i>Phillyrea angustifolia</i>	F	1	35 (100)	12	12 (100)	-
<i>Pistacia lentiscus</i>	F	1	22 (80)	13	13 (80)	-
<i>Rhamnus lycioides</i>	F	1.6	63 (30)	26	16 (30)	-
<i>Rosmarinus officinalis</i>	D	2.9	4 (20)	2	0.6 (59)	+
<i>Rubus ulmifolius</i>	F	40.4	213 (30)	87	2 (30)	-
<i>Smilax aspera</i>	F	1.4	78 (100)	51	36 (140)	-
<i>Stauracanthus genistoides</i>	D	2.5	59 (15)	13	5 (38)	+
<i>Ulex minor</i>	D	2.1	22 (20)	7	3 (35)	+
<i>Ulex parviflorus</i>	D	2	47 (10)	12	6 (20)	+

<sup>1</sup> D, dry fruits; F, fleshy, vertebrate-ingested fruits.

ber and flower size (dry weight); this relationship can be easily appreciated in Figure 1 ( $r = -0.826$ ,  $N = 27$ ,  $P < 0.001$ ).

Damage of flowers by insect predators, mostly noctuid larvae, coleopteran larvae, and other unidentified insects, was observed in only four species (Table 1).

#### FRUIT BIOLOGY

Table 2 summarizes various characteristics of the fruits in our set of mediterranean plant species. Fruit production in *Thymus tomentosus* was so sparse that we were unable to gather a reasonable sample of fruits and seeds; this species has therefore been excluded from the analyses. According to the way in which their seeds are dispersed our taxa are easily divided in two groups: those whose seeds are dispersed by vertebrates (13 taxa) and those whose seeds are dispersed by the wind or in a largely passive way (16 taxa). The former

have fleshy fruits, while the latter have dry fruits (mostly capsules, legumes, or achenes). Seed collecting by ants has been observed in a few taxa, but data are not conclusive enough to recognize a third (ant-dispersed) class. Most vertebrate-dispersed plant species in the sample have ornithochorous diaspores (C. M. Herrera, 1984a).

Mean number of seeds per fruit ranges between 1 and 51, and the fruit size (fruit dry weight) between 0.6 mg (*Helichrysum picardii*) and 1,364 mg (*Chamaerops humilis*). The lightest seeds are those of *Erica ciliaris* ( $2 \times 10^{-2}$  mg) and the heaviest those of *Chamaerops humilis* (781 mg). Predation of fruits, mainly by Curculionidae, larvae of Tortricidae, Noctuidae, and parasitic hymenopterans, is far more common than flower predation (55% and 13% of species, respectively). Damage by predators was observed more frequently on dry than on fleshy fruits ( $G = 4.02$ ,  $df = 1$ ,  $P < 0.05$ ).

TABLE 3. Results of independence tests performed between the type of fruit (dry or fleshy) and other variables of flowers and fruits. Class intervals considered were weight of fruit, less than 20 mg, 20–40 mg, 40–60 mg, or more than 60 mg; weight of the individual seed, less than 10 mg, or more than 10 mg; number of seeds per fruit, less than 2, 2–4, or more than 4.

Independence of Fruit Type	<i>G</i>	df	<i>P</i>
Sexuality (hermaphroditism, dioecy)	11.72	1	<0.001
Weight of fruit	8.04	3	<0.05
Weight of individual seed	23.32	1	<0.001
Seeds per fruit	13.85	2	<0.001

*G*, value of the statistic in the *G* test of independence; df, degrees of freedom.

Results of tests for the independence of fruit type and a few variables of flowers and fruits are given in Table 3. There is a significant tendency for species with hermaphroditic flowers to produce dry fruits, and for species with unisexual flowers to produce fleshy fruits. The independence hypothesis of fruit type and breeding system (Bawa, 1980) is thus rejected (Table 3). The only gynodioecious taxon in the sample has been included (conservatively) in the dioecious class for this analysis. The independence hypothesis for the type of fruit and the variables weight of fruit, weight of an individual seed, and seeds per fruit are all rejected. In fact, fleshy fruits tend to be, on average, heavier than dry ones ( $U = 185.5$ ,  $N = 16, 13$ ,  $P < 0.05$ ) and to have fewer and heavier seeds ( $U = 203$ ,  $N = 16, 13$ ,  $P < 0.001$ ). Note that we are reporting *dry weights*, so that differences are not due to the high water content of fleshy, vertebrate-ingested fruits.

Fruiting intensities for 28 of the studied species can be seen in Table 4. Data are not available for two dioecious species, *Corema album* and *Rhamnus lycioides*. Fruit production after exclusion of pollinators is also reported for hermaphroditic taxa. Percent of fruit production in open pollinated flowers ranged between 2% for *Thymus tomentosus* and *Daphne gnidium*, and 92% for *Halimium commutatum*. Bagging of flowers in most cases had a clear effect of decreasing fruit production—to levels as low as 0–1% in 15 species. There was just one taxon that was unaffected by exclusion of pollinators (*Daphne gnidium*, 2% fruit production under both treatments). Some fruit was produced (10–31%) in bagged flowers of a few taxa (*Calluna vulgaris*,

*Erica scoparia*, *Myrtus communis*, and *Rosmarinus officinalis*), but even in such cases pollinating vectors were needed for fruiting to arrive at its maximum.

#### REPRODUCTIVE TRADE-OFFS

Figure 2 shows the relationship between percent fruiting and the quotient of the fruit dry weight to the flower dry weight (fruit : flower size ratio hereafter), which indicates about how high the increase in size is from the first reproductive unit to the second. This variable will be employed below to investigate some patterns of reproductive allocation in our set of species. A highly significant negative relationship exists between percent fruit production and fruit : flower size ratio ( $r = -0.6780$ ,  $N = 26$ ,  $P < 0.001$ , log transformed data). Thus species in which there is a great increase in dry weight during the transition from flower to fruit are those with the lowest percent fruiting, whereas species in which this process involves little gain in weight have relatively greater fruiting success.

Species known to perform vegetative regeneration (sprouting) are distinguished from nonsprouting ones in Table 4, and their respective distribution in the relationship defined by percent fruit production and fruit : flower size ratio is shown in Figure 2. Sprouting taxa tend to have low values of fruiting and high values of fruit : flower size ratio. Mean percent fruit production is not, however, significantly different for sprouting and nonsprouting taxa ( $U = 109$ ,  $N = 14, 12$ ,  $P > 0.2$ ); differences in mean dry weight increase from flower to fruit are weakly significant ( $U = 117.5$ ,  $P > 0.05$ ). Species in the Ericaceae lower the coherence of the sprouting group, since they are well-known sprouters but have relatively low fruit : flower size ratios. If the Ericaceae are removed, the sprouting group is entirely composed of taxa with few-seeded, vertebrate-ingested fruits; with the exclusion of ericaceous taxa, the nonsprouting group overlaps entirely with the dry fruit group, and the sprouting group does likewise with the fleshy fruit group. Differences in mean percent fruit production and fruit : flower size ratio are now significant ( $U = 101.5$ ,  $P < 0.05$ ;  $U = 116.5$ ,  $P < 0.002$ ,  $N = 12, 11$ , respectively).

Figure 1 shows an inverse relationship between the number of flowers at peak blooming and flower dry weight. Both sprouting and nonsprouting species are evenly distributed along this continuum, so that mean number of flowers at

TABLE 4. Fruit production in open pollinated and bagged flowers of the studied species. Numbers in parentheses indicate the number of flowers, and N the number of plants. The sample of the only gynodioecious species (*Thymus tomentosus*) includes three hermaphrodites and four female plants. Species known to be capable of sprouting are marked with an asterisk.

Species	Fruit Production (%)		N
	Open Pollinated	Bagged	
<i>Armeria velutina</i>	59 (478)	3 (476)	5
<i>Asparagus aphyllus*</i>	24 (804)	—	6
<i>Calluna vulgaris*</i>	88 (100)	24 (50)	5
<i>Chamaerops humilis*</i>	4 (4,560)	—	7
<i>Cistus libanotis</i>	55 (5,822)	0.2 (538)	4
<i>Cistus salvifolius</i>	50 (3,014)	0 (92)	10
<i>Cytisus grandiflorus</i>	12 (150)	0 (134)	4
<i>Daphne gnidium*</i>	2 (23,749)	2 (2,660)	10
<i>Erica ciliaris*</i>	45 (147)	1 (105)	10
<i>Erica scoparia*</i>	89 (85)	31 (65)	5
<i>Halimium commutatum</i>	92 (100)	0 (100)	5
<i>Halimium halimifolium</i>	41 (70)	1 (1,259)	5
<i>Helianthemum croceum</i>	—	0 (171)	3
<i>Helichrysum picardii</i>	68 (1,308)	1 (1,443)	5
<i>Lavandula stoechas</i>	69 (200)	0.4 (1,040)	10
<i>Lonicera periclymenum*</i>	8 (1,537)	4 (211)	4
<i>Myrtus communis*</i>	68 (857)	23 (78)	4
<i>Osyris alba*</i>	7 (1,385)	—	8
<i>Osyris quadripartita*</i>	5 (2,400)	—	5
<i>Phillyrea angustifolia*</i>	14 (1,229)	0 (735)	5
<i>Pistacia lentiscus*</i>	16 (1,368)	—	5
<i>Rosmarinus officinalis</i>	31 (256)	10 (797)	5
<i>Rubus ulmifolius*</i>	78 (931)	0 (158)	10
<i>Smilax aspera*</i>	9 (4,053)	—	5
<i>Stauracanthus genistoides</i>	40 (115)	0.2 (651)	4
<i>Thymus tomentosus</i>	2 (210)	0 (210)	7
<i>Ulex minor</i>	16 (238)	0 (221)	10
<i>Ulex parviflorus</i>	5 (310)	0 (471)	5

peak blooming is not significantly different between them ( $U = 101$ ,  $P > 0.1$ ); neither is mean flower dry weight significantly different ( $U = 113.5$ ,  $P > 0.1$ ,  $N = 14$ , 13). Both sprouting and nonsprouting taxa may be many- and small- or few- and big-flowered.

#### DISCUSSION

The 30 mediterranean plant species studied represent a relatively small sample of the regional flora (more than 2,000 taxa for southern Spain, of which nearly 300 are woody). Furthermore, shrublands have many different and diverse species compositions in southern Spain, depending on elevation, rainfall, edaphic factors, etc., so that the results reported here should be extended only with caution to other scrub communities in the region. Nevertheless many of the

studied taxa are widespread, and the community they form is undoubtedly a clear example of coastal scrub on sandy soils, which is characteristic of other areas in southern Spain.

In the studied community a sizeable heterogeneity in reproductive traits was likely to occur, since 30 plant species were distributed among 17 families. However, certain groups (virtually Cistaceae, Leguminosae, Ericaceae, and Labiatae) contributed with more taxa to the sample than did others. Hence a phylogenetic component in the reproductive patterns recognized should not be ruled out, in addition to an ecological component and to the fact that the plants form a steady, long-lasting community achieving reproduction year after year. Several aspects in the reproductive patterns are not restricted to our particular community. The relative dominance of taxa in which nectar yield is low or even zero,

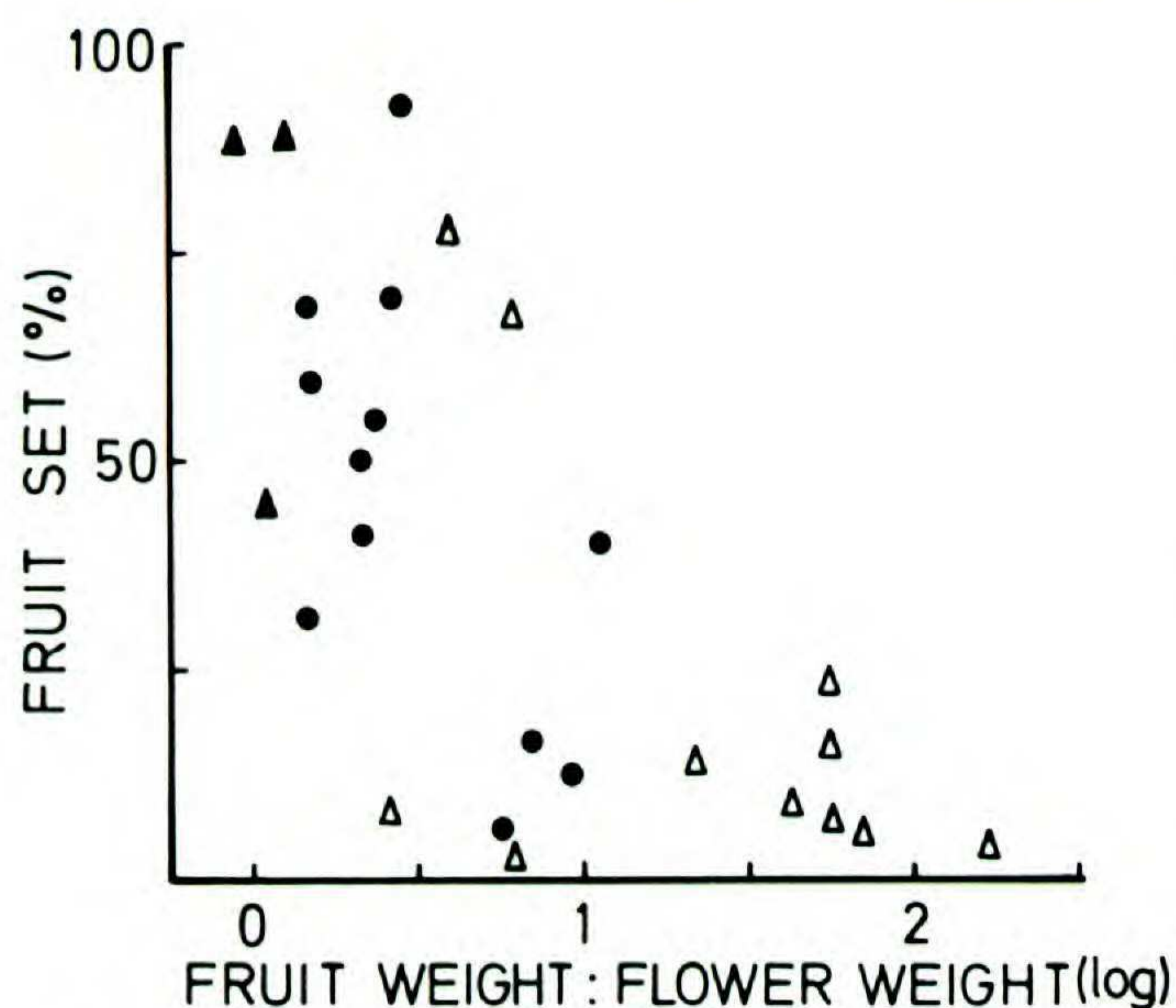


FIGURE 2. Relationship between fruit:flower dry weight ratio and percent fruiting for 26 scrub taxa. Triangles = sprouting species; circles = nonsprouting species; black triangles = species in the family Ericaceae.

for example, is general in the region (J. Herrera, 1985). The consequences of this factor upon the pollination relationships will be dealt with elsewhere (J. Herrera, in prep.). Dispersal by inanimate or vertebrate agents creates a dichotomy that is also found in other mediterranean-type communities (Bullock, 1978, chaparral; C. M. Herrera, 1984b; Jordano, 1984, southern Spain). As has been reported in other woody communities (Reader, 1977; Ruiz-Zapata & Arroyo, 1978; Bawa, 1979; Bawa & Beach, 1983) pollinators are needed for maximum fruit production. Further investigations will determine the extent to which incompatibility systems occur in shrublands of southern Spain.

Sprouting is also a common regenerative strategy of woody plants in many and diverse ecosystems (James, 1984). It is particularly important in regions of a mediterranean-type climate that experience summer droughts and frequent fires. This aspect has received much attention in the Californian chaparral (Wells, 1969; Keeley, 1977), where two general reproductive strategies (in fact, extremes of a continuum) have been recognized: the "seeder" strategy consists of obligate seed reproduction and incapacity to form new stem sprouts after destruction of aerial parts; the "sprouters" can produce stem or root sprouts that enable repeated shoot production despite frequent damage (Malanson & Westman, 1985; see James, 1984, for an extensive review). It appears that both strategies also are found among sclerophyllous species of the Mediterranean Ba-

sin. In our community most plants fall clearly into one category or the other, although species in the Ericaceae could be easily included in both: they produce plenty of seeds and are also able to sprout, which was reported some time ago for *Calluna vulgaris* (Kayll & Gimingham, 1965).

It has been hypothesized that pollination-reproduction variables may be associated with each of the sprouting or nonsprouting strategies. In seeders, for example, the pollination system must be efficient enough to assure the release of numerous seeds (which could open a way to self-compatibility), produce numerous flowers highly attractive to pollinators, and offer a greater reward per flower than sprouters (Carpenter & Recher, 1979). In contrast, sprouting taxa are proposed to have a high rate of outcrossing, although often with a low production of flowers, which would be relatively low rewarding (Fulton & Carpenter, 1979; Carpenter & Recher, 1979). These hypotheses are supported in part by our data.

A high rate of outcrossing has to be expected in the sprouting group of species, since many dioecious taxa are included in that group. There are no evident signs, however, of a high incidence of self-pollination in the nonsprouting group. In contrast, mean percent fruit production was significantly higher for nonsprouters than for sprouting species, which confirms the hypothesis outlined above. Low pollination efficiency due to unisexuality can be reasonably proposed to explain low fruit production in the sprouting group, but we wish to put forward a complementary view. Percent of fruit production was found to be inversely related to fruit:flower size ratio (i.e., the increase in mass needed to produce a fruit from a flower). Such a relationship suggests the existence of a trade-off between the energy that a plant allocates to an individual fruit or seed and the number it can successfully form. Low fruit production in vertebrate-dispersed, big-seeded species may reflect low pollination success and/or the impossibility of developing every fruit with pollinated ovules, due to the relatively high costs involved in the ripening process. It has been demonstrated, for example, that some species experience low fruit production despite good levels of pollination, which is apparently due to intrinsic regulatory mechanisms (Lloyd, 1980; Wyatt, 1981; Casper & Wiens, 1981; Casper, 1983; Bookman, 1983; Bawa & Webb, 1984; see Stephenson, 1981, for a review). Flower size and number showed a negative relationship too,



but the predicted tendency for sprouting taxa to appear at one end of this continuum has not been detected by us.

Wells (1969) pointed out that the capacity to sprout vegetatively from underground parts is probably an ancestral trait. James (1984), however, suggested that sprouting cannot always be seen as an ancestral trait in woody dicotyledons. In the present study the capacity to sprout is associated with other traits, such as the production of fleshy, vertebrate-ingested fruits, heavy seeds, and low fruit production, along with a relatively high incidence of dioecy (species in the genera *Asparagus*, *Chamaerops*, *Lonicera*, *Osyris*, *Pistacia*, *Rhamnus* and *Smilax*, for example). This group of taxa has subtropical affinities: sclerophyllous species in these genera existed well before the Pleistocene and the evolution of true mediterranean climatic conditions (Raven, 1973; Axelrod, 1975; Pons, 1981). In contrast, species in the genera *Armeria*, *Cistus*, *Cytisus*, *Halimium*, *Lavandula*, *Rosmarinus*, or *Thymus* are nonsprouters; and the high number of taxa endemic to the Mediterranean Basin makes clear that species in these genera originated much more recently (Quezel, 1978, 1981; Pons, 1981). The capacity to sprout is thus lacking in the typically mediterranean taxa but is present in the more ancient, pre-mediterranean ones. This supports the view of Wells (1969) that sprouting is an ancestral trait, and it may indicate that only those "tertiary flora" subtropical sclerophyllous taxa with a capacity to sprout were able to survive the shift to seasonal dryness associated with the mediterranean climate.

#### LITERATURE CITED

- ALLIER, C. F., F. GONZALEZ-BERNALDEZ & L. RAMIREZ-DÍAZ. 1974. Reserva Biológica de Doñana. Ecological Map. Estación Biológica de Doñana, CSIC, Sevilla, Spain.
- AXELROD, D. I. 1975. Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Ann. Missouri Bot. Gard.* 62: 284–334.
- BAWA, K. S. 1979. Breeding systems of trees in a tropical wet forest. *New Zealand J. Bot.* 17:521–524.
- . 1980. Evolution of dioecy in flowering plants. *Ann. Rev. Ecol. Syst.* 11:15–39.
- & J. H. BEACH. 1983. Self-incompatibility systems in the Rubiaceae of a tropical lowland wet forest. *Amer. J. Bot.* 70: 1281–1288.
- & P. A. OPLER. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167–179.
- & C. J. WEBB. 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *Amer. J. Bot.* 71: 736–751.
- BOLTEN, A. B., P. FEINSINGER, H. G. BAKER & I. BAKER. 1979. On the calculation of sugar concentration in flower nectar. *Oecologia (Berl.)* 41: 301–304.
- BOOKMAN, S. S. 1983. Costs and benefits of flower abscission and fruit abortion in *Asclepias speciosa*. *Ecology* 64: 264–273.
- BULLOCK, S. H. 1978. Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madroño* 25: 104–105.
- CARPENTER, F. L. & H. F. RECHER. 1979. Pollination, reproduction and fire. *Amer. Naturalist* 113: 871–879.
- CASPER, B. B. 1983. The efficiency of pollen transfer and rates of embryo initiation in *Cryptantha* (Boraginaceae). *Oecologia (Berl.)* 59: 262–268.
- & D. WIENS. 1981. Fixed rates of random ovule abortion in *Cryptantha flava* (Boraginaceae) and its possible relation to seed dispersal. *Ecology* 62: 866–869.
- CODY, M. L. & H. A. MOONEY. 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. *Ann. Rev. Ecol. Syst.* 9: 265–321.
- CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.
- FAEGRI, K. & L. VAN DER PIJL. 1979. Principles of Pollination Ecology, 3rd edition. Pergamon Press, Oxford.
- FRANKIE, G. W., H. G. BAKER & P. A. OPLER. 1974. Comparative phenological studies in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- , W. A. HABER, P. A. OPLER & K. S. BAWA. 1983. Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. Pp. 411–447 in C. E. Jones & R. J. Little (editors), *Handbook of Experimental Pollination Biology*. Scientific & Academic Editions, New York.
- FULTON, R. E. & F. L. CARPENTER. 1979. Pollination, reproduction and fire in California *Arctostaphylos*. *Oecologia (Berl.)* 38: 147–157.
- HEITHAUS, E. R. 1974. The role of plant-pollinator interactions in determining community structure. *Ann. Missouri Bot. Gard.* 61: 657–691.
- HERRERA, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? *Amer. Naturalist* 118: 896–907.
- . 1984a. A study of avian frugivores, bird-dispersed plants and their interactions in mediterranean scrublands. *Ecol. Monogr.* 54: 1–23.
- . 1984b. Patrones morfológicos y funcionales en plantas del matorral mediterráneo del sur de España. *Studia Oecologica* 5: 7–34.
- HERRERA, J. 1985. Nectar secretion patterns in southern Spanish mediterranean scrublands. *Israel J. Bot.* 34: 47–58.
- INOUE, D. W., N. D. FAVRE, J. A. LANUM, D. M. LEVINE, J. B. MEYERS, M. S. ROBERTS, F. C. TSAO & Y. Y. WANG. 1980. The effect of nonsugar nectar constituents on estimates of nectar energy content. *Ecology* 61: 992–995.
- JAMES, S. 1984. Lignotubers and burls—their structure, function and ecological significance in mediterranean ecosystems. *Bot. Rev.* 50: 225–266.
- JORDANO, P. 1982. Migrant birds are the main seed

- dispersers of blackberries in southern Spain. *Oikos* 38: 183–193.
- . 1984. Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana. Ph.D. Thesis. University of Sevilla, Sevilla, Spain.
- KAYLL, A. J. & C. H. GIMINGHAM. 1965. Vegetative regeneration of *Calluna vulgaris* after fire. *J. Ecol.* 53: 729–734.
- KEELEY, J. E. 1977. Seed production, seed populations in soil and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. *Ecology* 58: 820–829.
- KEVAN, P. G. 1972. Insect pollination of high Arctic flowers. *J. Ecol.* 60: 831–847.
- KRUGER, F. J. 1981. Seasonal growth and flowering rhythms: South African heathlands. Pp. 1–4 in R. L. Specht (editor), *Ecosystems of the World. Heathlands and Related Shrublands*. Elsevier, Amsterdam.
- KUMMEROV, J. 1983. Comparative phenology of mediterranean-type plant communities. Pp. 300–317 in F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis (editors), *Mediterranean-type Ecosystems*. Springer-Verlag, Berlin.
- LLOYD, D. G. 1980. Sexual strategies in plants. 1. A hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytol.* 86: 69–79.
- MALANSON, G. P. & W. E. WESTMAN. 1985. Post fire succession in California coastal sage scrub: the role of continual basal sprouting. *Amer. Midl. Nat.* 113: 309–318.
- MOLDENKE, A. R. 1975. Niche specialization and species diversity along a California transect. *Oecologia (Berl.)* 21: 219–242.
- MOONEY, H. A. & E. L. DUNN. 1970. Convergent evolution of mediterranean-climate evergreen sclerophyll shrubs. *Evolution* 24: 292–303.
- & D. J. PARSONS. 1973. Structure and function of the California chaparral. Pp. 83–112 in F. di Castri & H. A. Mooney (editors), *Mediterranean-type Ecosystems*. Springer-Verlag, New York.
- , ——— & J. KUMMEROV. 1974. Plant development in mediterranean climates. Pp. 255–267 in H. Lieth (editor), *Phenology and Seasonality Modeling*. Springer-Verlag, New York.
- MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering times. *Oikos* 22: 398–402.
- OPLER, P. A., H. G. BAKER & G. W. FRANKIE. 1980. Plant reproductive characteristics during secondary succession in neotropical lowland forest ecosystems. *Biotropica (Tropical Succession)* 12: 40–46.
- POJAR, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Can. J. Bot.* 52: 1819–1834.
- PONS, A. 1981. The history of the mediterranean shrublands. Pp. 131–138 in F. di Castri, D. W. Goodall & R. L. Specht (editors), *Mediterranean-type Ecosystems*. Elsevier, Amsterdam.
- PRIMACK, R. B. 1983. Insect pollination in the New Zealand mountain flora. *New Zealand J. Bot.* 21: 317–333.
- QUEZEL, P. 1978. Analysis of the flora of the Mediterranean and Saharan Africa. *Ann. Missouri Bot. Gard.* 65: 479–534.
- . 1981. Floristic composition and phytosociological structure of sclerophyllous matorral around the Mediterranean. Pp. 107–121 in F. di Castri, D. W. Goodall & R. L. Specht (editors), *Mediterranean-type Ecosystems*. Elsevier, Amsterdam.
- RAVEN, P. H. 1973. The evolution of mediterranean floras. Pp. 213–224 in F. di Castri & H. A. Mooney (editors), *Mediterranean-type Ecosystems*. Springer-Verlag, Berlin.
- READER, R. J. 1977. Bog ericads flowers: self-compatibility and relative attractiveness to bees. *Can. J. Bot.* 55: 2279–2287.
- RIVAS-MARTÍNEZ, S., M. COSTA, S. CASTROVIEJO & E. VALDÉS. 1980. Vegetación de Doñana (Huelva, España). *Lazaroa* 2: 5–189.
- RUIZ-ZAPATA, T. & M. T. K. ARROYO. 1978. Plant reproductive ecology of a secondary deciduous forest in Venezuela. *Biotropica* 10: 221–230.
- SPECHT, R. L. 1969. A comparison of the sclerophyllous vegetation characteristics of mediterranean type climates in France, California, and southern Australia. *Austral. J. Bot.* 17: 277–292.
- , R. W. RODGERS & A. J. M. HOPKINS. 1981. Seasonal growth and flowering rhythms: Australian heathlands. Pp. 5–13 in R. L. Specht (editor), *Ecosystems of the World. Heathlands and Related Shrublands*. Elsevier, Amsterdam.
- STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Ann. Rev. Ecol. Syst.* 12: 253–279.
- WELLS, P. V. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. *Evolution* 23: 264–267.
- WYATT, R. 1981. The reproductive biology of *Asclepias tuberosa* II: factors determining fruit set. *New Phytol.* 88: 375–385.